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Megachile glaesaria, the First Megachilid Bee Fossil from Amber (Hymenoptera: Megachilidae)

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ABSTRACT

A bee of the family Megachilidae is recorded as an amber inclusion for the first time. The individual is representative of a primitive new subgenus and species of the genus *Megachile*, *Chalicodoma* subgeneric complex. ***Megachile glaesaria***, new species, is described and figured from a single female preserved in Miocene Dominican amber. The subgenus ***Chalicodomopsis***, new subgenus, is proposed for this taxon. The fossil appears most similar to species of the subgenus *Chelostomoides* and, in particular, the recent *M. manni* Mitchell, an exceedingly uncommon species presently known only from southern Arizona. The known fossil Megachilidae are briefly reviewed (none are older than the Eocene-Oligocene) and recent debates on early megachilid nest evolution considered.

INTRODUCTION

Bees of the genus *Megachile* Latreille (1802) are most widely known as the leaf-cutters, but those of the *Chalicodoma* group of subgenera do not cut leaves and instead collect resins or mud for use in making cells or the lining of cells within the nest (Hacker, 1915; Hicks, 1927; Messer, 1984; O'Toole and Raw, 1991). Nests are constructed in abandoned insect borings in dead wood or by cementing materials together on exposed walls. Cells are made by lining the cavity with resin and then sealing each with either a leaf fragment covered with resin or, more frequently, with resin alone (sometimes intermixed with wood particles).

Species of *Megachile* occur throughout the world but are most diverse in the Eastern Hemisphere. Together with the parasitic genus *Coelioxys* Latreille (1809), *Megachile* constitutes the tribe Megachilini. Previously the tribe contained several genera (e.g., Michener, 1962; Mitchell, 1980) but under the classificatory scheme preferred by most

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authors today (e.g., Michener, in press; Michener et al., 1994; Schwarz et al., 1996; Müller et al., 1997) the genera *Chalicodoma* Lepeletier de Saint Fargeau (1841) and *Creightonella* Cockerell (1908a) are included in an expanded *Megachile*. However, some authors still recognize these genera and their constituent subgenera as separate from *Megachile* (e.g., Snelling, 1990; Rasmont et al., 1995). Of the subgenera constituting the *Chalicodoma* group, only two occur natively in the New World. The subgenus *Chelostomoidella* Snelling (1990) contains only the type species, *Megachile spinotulata* Mitchell (1934), and is distributed from southern California to western Texas and south into Baja California and northern Mexico proper. The subgenus *Chelostomoides* Robertson (1901) is much larger with over two dozen species ranging from southern Canada to Peru but with its greatest diversity in North America. The fossil species presented herein is most similar to this latter group and is presumably the basal most taxon of *Chalicodoma* and thereby of *Megachile* as a whole.

Today, only three species of the *Chalicodoma* group are native to the Greater Antilles, these being *M. armaticeps* (Cresson, 1869) from the island of Cuba, and *M. jamaicae* (Raw, 1984) and *M. rawi* Engel[2] from Jamaica. Although three additional *Chalicodoma* species can be found in the West Indies, these are all adventive, having been introduced from Africa and India (Mitchell, 1980; Snelling, 1990; Genaro, 1997). The species described below is the first representative of the *Chalicodoma* group from the geological record and is the first definitive megachilid fossil described from amber.

Amber of the Dominican Republic is 15–20 Ma, placing it in the Miocene epoch (Burdigalian stage) (Iturralde-Vinent and MacPhee, 1996, 1999). Presently there are 11 bee species in Dominican amber representing every bee family except Melittidae and Stenotritidae (table 1); the latter occurs only in Australia.[3] Interestingly, those groups that collect plant resins account for 36% of the specific diversity of the Dominican amber fauna as it is currently understood. Species of Protandrenini, Chilicolini, and Halictinae are not known to collect resins and therefore seem unlikely candidates for entrapment and preservation in amber. The halictines, at least, are one of the most common components of many modern bee faunas, and it is possible that if this diversity were mirrored in the ancient forests of Hispaniola, sheer abundance might account for their specific diversity in amber. The eusocial meliponines are the most common bees in Dominican amber but at present are known only on the basis of one species, although two additional species are currently being described (Camargo et al., in prep.). It is possible that the resin-handling ability of these other groups (e.g., Euglossini, Meliponini) helps them to avoid being caught in sap and thus preserved in amber.

Acknowledgments

I am sincerely grateful to Dott. Ettore Morone for once again allowing me to study the spectacular inclusions from his collection, and to David A. Grimaldi for recognizing the significance of the specimen and for acting as courier of material between Morone and myself. I am further indebted to Dave for his unflagging support of my studies and advice in matters paleontological. David A. Grimaldi, Charles D. Michener, Molly G. Rightmyer, Jerome G. Rozen, Jr., and two anonymous reviewers read over versions of the manuscript and provided criticisms that significantly improved its presentation. I am thankful for their willingness to share their time and knowledge with me. I benefited enormously from several discussions with Michener who helped me recognize the subtle plesiomorphic differences of this fossil from extant *Megachile* as well as to one of the anonymous reviewers who also recognized several differences from living *Chelos-*

[2] *Megachile* (*Chelostomoides*) *rawi* Engel, *nomen novum pro Chelostomoides pedalis* Raw, 1984, *nomen preoccupatum*, junior secondary homonym in *Megachile* (*nec Megachile pedalis* Fox, 1891). Etymology: Named in honor of the original author, Dr. Anthony Raw.

[3] It should be noted, however, that the present-day occurrence of stenotritids in Australia certainly does not exclude them from being discovered in New World amber. For example, the ant genus *Leptomyrmex*, also from Australia, has been discovered in Dominican amber.

TABLE 1
Described Bees from Miocene Dominican Amber

Taxa	References
ANDRENIDAE: Panurginae	
Protandrenini	
Heterosarus eickworti Rozen	Rozen, 1996
APIDAE: Apinae	
Euglossini	
Eufriesea melissiflora (Poinar)	Poinar, 1998; Engel, 1999
Euglossa moronei Engel	Engel, 1999
Meliponini[a]	
Proplebeia dominicana (Wille and Chandler)	Wille and Chandler, 1964 Michener, 1982
COLLETIDAE: Xeromelissinae[b]	
Chilicolini	
Chilicola (*Hylaeosoma*) *gracilis* Michener and Poinar	Michener and Poinar, 1996
MEGACHILIDAE: Megachilinae	
Megachilini	
Megachile (*Chalicodomopsis*) *glaesaria* Engel	Present study
HALICTIDAE: Halictinae[c]	
Augochlorini	
Neocorynura electra Engel	Engel, 1995
Oligochlora eickworti Engel	Engel, 1996
Oligochlora grimaldii Engel	Engel, 1997
Oligochlora micheneri Engel	Engel, 1996
Halictini	
Eickwortapis dominicana Michener and Poinar	Michener and Poinar, 1996

[a] Two new species of *Proplebeia* stingless bees are currently being described by Prof. J. M. F. de Camargo and associates (Camargo et al., in prep.).

[b] A second xeromelissine has been recognized and will be described in a forthcoming paper (Engel, in press).

[c] Additional halictines have recently been identified and will be treated in forthcoming papers on fossil bees (Engel, in prep.; Engel and Rightmyer, in prep.).

tomoides species. My work at the AMNH is supported by the generosity of two gentlemen: Robert G. Goelet and Jerome G. Rozen, Jr.

TERMINOLOGY

Morphological terminology generally follows that of Michener (1944). The abbreviations F, OD, S, and T are used for flagellomere, ocellar diameter (based on the median ocellus), metasomal sternum, and metasomal tergum, respectively. Measurements (in millimeters) were made with an ocular micrometer and should be considered approximations since the optimal angle for particular measures was not always achievable through the amber.

SYSTEMATIC PALEONTOLOGY

GENUS *MEGACHILE* LATREILLE *CHALICODOMA* GROUP

Chalicodomopsis, new subgenus

TYPE SPECIES: *Megachile* (*Chalicodomopsis*) *glaesaria*, new species.

DIAGNOSIS: This group appears most similar to *Chelostomoides* but differs most notably in the sharply angled preoccipital margin, the ridge and groove above the antennal socket, the broadly rounded labral apex, the relatively short stigma, and 2m-cu being confluent with 2r-m.

DESCRIPTION: **Female.** Body without maculations of any sort. Mandible quadridentate, lower tooth smallest, no cutting edges be-

tween teeth (fig. 3); length of dentate apical margin of mandible less than one-half length of lower mandibular margin. Labrum broadly U-shaped (fig. 2), apical margin broadly rounded, medial length about equal to basal width; surface smooth and impunctate; widely scattered short, erect hairs on surface, slightly longer along lateral margins. Strong ridge on inner border of antennal socket extending posteriorly to form short groove into which scape can recline (figs. 1, 2), groove length only one-third scape length, ridge forming slight lamella overhanging antennal socket on lower half of groove. Preoccipital area not carinate but very sharply angled. Scutellum flat, sharply angled between dorsal and posterior surfaces, projecting posteriorly over metanotum and propodeum; preaxilla sloping with short hairs; omalus absent, no distinct separation between anterior and lateral surfaces of mesepisternum, instead very gently rounded; narrow dorsal lamella apparently on metepisternum. Claw with small inner tooth, much shorter than outer tooth; arolia absent. Stigma about as long as broad; 2m-cu confluent with 2r-m; first submarginal cell approximately equal in length to second submarginal cell. Metasoma approximately parallel-sided (fig. 1). **Male.** Unknown.

ETYMOLOGY: The new genus-group name is a derivative of *Chalicodoma*, the group of *Megachile* to which it belongs, presumably as one of the most primitive members.

COMMENTS: Note that details of the wing are difficult to see in the fossil. Some features of this group are plesiomorphic traits of the tribe and suggest that *Chalicodomopsis* may be the basal most member of the *Chalicodoma* group and perhaps of the tribe Megachilini as a whole. Such features include the small inner tooth of the claws, the stigma being as long as broad (intermediate between Megachilini and Anthidiini), and the confluence of 2r-m and 2m-cu (intermediate between Megachilini and Anthidiini). For these and other reasons it may be advisable to place *Chalicodomopsis* into its own tribe (Chalicodomopsini) once a cladistic analysis of Megachilidae has been finalized in connection with a monograph of the Baltic amber bees (Engel, in prep.).

Megachile (*Chalicodomopsis*) *glaesaria*, new species

Figures 1–3

DIAGNOSIS: Owing to the extreme similarity of this group and species to *Chelostomoides*, it is differentiated from the species of this subgenus with which it might be most readily confused. Interestingly, this species appears most similar to the exceedingly rare *M. manni* Mitchell (1934) from southern Arizona. Both species have the abrupt apical lip of female T6 which is triangular in dorsal aspect and the relatively simple clypeal apex. Aside from the subgeneric characters given above, the new species can be distinguished from *M. manni* by the upper half of the gena being much broader than the compound eye in profile (gena narrower than the compound eye in *M. manni*), distance between lateral ocelli and compound eye much shorter than length of vertex (these distances are approximately equal in *M. manni*), T6 not obscured by dense pubescence, postgena impunctate (finely punctate in *M. manni*), scutellar punctures as those of mesoscutum (finer than mesoscutal punctures in *M. manni*), wing membrane fuscous (subhyaline in *M. manni*), brown tibial spurs (pale yellow in *M. manni*), and fuscous scopal hairs (ochraceous in *M. manni*).

DESCRIPTION: **Female.** Total body length 9.4; forewing length 6.1; head width 3.2, length 2.4; scape length 0.8; intertegular distance 2.4, mesoscutal length 1.9; metasoma length 4.3. Mandible smooth except outer basal quarter with fine punctures separated by one to two times puncture width; mandible of uniform width across its entire length. Apical margin of clypeus simple, very weakly concave where joining labrum; apical margin of clypeus with width about 17 times greater than medial length, only about 1½ times longer than basal labral width; apical margin of clypeus impunctate and shining; anterior-facing surface medially longer than on lateral margins, which are about as long as medial length of impunctate apical margin (fig. 3), borders with coarse punctures separated by about one puncture width or less, integument between smooth and shining; near mandibular base punctures like those of most of clypeal surface, punctures separated

Fig. 1. Photomicrograph of female holotype of *Megachile glaesaria*, n. sp., dorsal aspect (Photograph by the author).

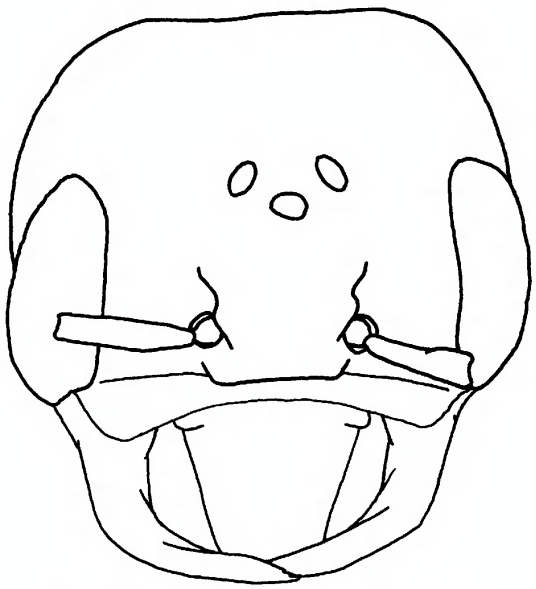

Fig. 2. Slightly oblique, dorsal aspect of head of *Megachile glaesaria*, n. sp.; setae and punctation omitted.

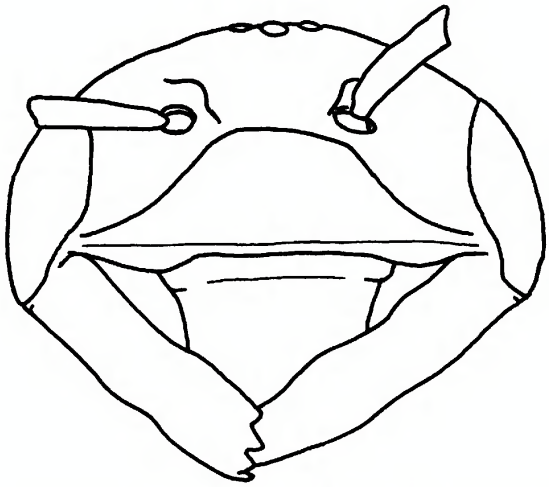

Fig. 3. Frontal aspect of head of *Megachile glaesaria*, n. sp.; setae and punctation omitted.

by about one puncture width. Supraclypeal area much wider than long, slightly protuberant. Punctures on face and vertex coarse, separated by less than one puncture width, nearly contiguous, integument between (where evident) smooth. Upper half of gena punctured as on vertex, lower half with punctures becoming more widely spaced, separated by about one puncture width, integument between smooth. Postgena impunctate. Median ocellus separated from lateral ocellus by one OD; distance between lateral ocelli about 2½ OD; distance from lateral ocellus to compound eye nearly five OD; vertex long, nearly seven OD in length (figs. 1, 2). Compound eyes only weakly divergent below. Head broader than long. Compound eyes separated by more than eye length. Distance from antennal socket to inner border of compound eye about two-thirds scape length; distance between antennal sockets equal to scape length; antennal sockets positioned just below middle of compound eyes. Antenna short; pedicel longer than F1; F2 slightly longer then F1; F3 slightly longer than F2. Pronotum, mesoscutum, scutellum, and pleura punctured as on vertex (fig. 1). Tegula oval and impunctate. Antenna cleaner without malus projecting from dorsal margin of vellum (perhaps broken?); metatibial spurs serrate; outer spur subequal in length to inner spur. Basal vein apparently confluent with cu-a, relatively straight. Terga punctured as on mesosoma (fig. 1) except on central discs of T2–5 where punctures are slightly weaker and more widely spaced, separated by about one puncture width; T2–5 with distinct basal depressions (referred to as "basal grooves" by Mitchell, 1934); T6 with abrupt apical lip, triangular in dorsal aspect; sterna apparently impunctate, weakly nodulate.

Integument appearing brassy except mandibles, labrum, clypeus, antennae, tegulae, and legs brown. Wing membrane fuscous; veins black. Metasoma slightly darker than remainder of body.

Pubescence fuscous; generally minute and sparse. Compound eyes bare. Surface of T6 not obscured by dense pubescence. Scopa present as a series of long, stout, hairs with a few minute branches on all metasomal sterna; pubescence of S1–2 unmodified. **Male.** Unknown.

HOLOTYPE: Female (M-2718), Miocene amber of the Dominican Republic; Morone Amber Collection, Turin, Italy.

PRESERVATION: The block of amber is roughly trapezoidal in dorsal view with the leading edge widest (about 3 cm). From this vantage point the left side proceeds posteriorly in about a direct line (approximately parallel to the bee preserved inside) for 2.5

cm where the posterior border of the block is 2 cm wide. The right side of the block is at an angle to the side opposite it and is about 2.7 cm long. The entire piece when viewed in profile is about 1.6 cm high. There is a small flower well anterior and to the right of the bee's head and two minute beetles behind and to the left of the bee (the flower and the beetles would be just outside the upper right and lower left corners of fig. 1). The bee is magnificently preserved with little mold or damage to the integument. There is some mold in the fissure separating the scutellum and mesoscutum, on the propodeum and anterior surface of T1, at the wing base, and scattered in other areas, but to a lesser degree. The bee is preserved with the body extended lengthwise (not bent between any of the tagmata) (fig. 1). The forelegs are projecting anteriorly along the sides of head, the midlegs are folded under the mesosoma, the left hind leg is extending away from the body below the bee, while the right hind leg is extended posterolaterally at an oblique angle (fig. 1). The left wings are at rest over the side of the metasoma, while the right wings are extended perpendicular to the body and folded longitudinally (fig. 1).

ETYMOLOGY: The specific epithet is derived from the Latin word *glaesarius*, meaning "of amber."

DISCUSSION

In keys to the subgenera of *Megachile* (or *Chalicodoma*), *M. glaesaria* will run to *Chelostomoides* from which it can be differentiated by the characters presented above. Snelling (1990) has given a key to the North American species of *Chalicodoma* (both *Chelostomoides* and *Chelostomoidella*) and *M. glaesaria* will run to *M. manni* in his key. The following couplet modifications and additions will properly incorporate *M. glaesaria* into Snelling's key to females of the *Chalicodoma* group:

27. Clypeus evenly convex, not strongly angulate across middle, apical margin variously excavated and denticulate or tuberculate 28
– Clypeus transversely angulate across middle, lower facet oblique and impunctate or nearly so, apical margin simple, straight or nearly so ..... 27′

27′. Clypeal apex straight; face without ridge or groove near antennal socket; ocellar-orbital distance equal to vertex length; upper gena narrower than compound eye; scopal hairs ochraceous; T6 densely pubescent, obscuring surface ... *M. manni* Mitchell
– Clypeal apex weakly concave; face with ridge and groove near antennal socket; ocellar-orbital distance shorter than vertex length; upper gena much broader than compound eye; scopal hairs fuscous; pubescence not obscuring surface of T6 ... . *M. glaesaria* Engel

The affinity of this species with a group from the southwestern United States is mirrored in some other Dominican amber insects. The bee *Heterosarus eickworti* Rozen (1996) shares affinities with extant species groups of *Heterosarus* from the southwestern United States, while the window fly *Metatrichia pria* Yeates and Grimaldi (1993) similarly has as its nearest relative a Nearctic species. The other Miocene bee species (table 1) all have affinities with species or groups from southern Mexico or further south. There is currently no hypothesis of phylogenetic relationships among *Chelostomoides* species or *Megachile* subgenera. The relatively simple clypeal structures of *M. manni* and *M. glaesaria* are presumably plesiomorphic traits, but the actual phylogenetic position of these taxa must remain speculative until a comprehensive cladistic study of *Megachile*, and the *Chalicodoma* group in particular, has been undertaken. The *Chalicodoma* group is the basal most group of *Megachile* and is perhaps paraphyletic with respective to the remainder of the *Megachile* subgenera.

There are presently 21 bee species reported from the geological record that are assigned to the Megachilidae (table 2), including the fossil presented herein. Most are from the Megachilinae, although one is currently placed in the subfamily Lithurginae. The subfamily Fideliinae is not at present known in the fossil record. Of the megachilines, ten are attributed to the Osmiini and six to the Anthidiini. The remaining four are assigned to the nominate tribe. All of these, except *M. glaesaria*, are compression fossils. Owing to the dubious nature of many of these fossils (particularly many of those from the Florissant deposits), I hesitate at this time to make

TABLE 2

Described Fossil Megachilidae[a,b]

(All are compression fossils except *Megachile glaesaria*, which is an amber inclusion.)

Taxa	References
FLORISSANT, COLORADO (EOCENE-OLIGOCENE)	
Anthidium exhumatum Cockerell	Cockerell, 1906
Anthidium scudderi Cockerell	Cockerell, 1906
Dianthidium tertiarium Cockerell[c]	Cockerell, 1906
Heriades bowditchi Cockerell	Cockerell, 1906
Heriades halictinus Cockerell	Cockerell, 1906
Heriades laminarum Cockerell	Cockerell, 1906
Heriades mersatus Cockerell	Cockerell, 1923
Heriades mildredae Cockerell	Cockerell, 1925a
Heriades priscus Cockerell	Cockerell, 1917
Heriades saxosus Cockerell	Cockerell, 1913
Lithanthidium pertriste Cockerell	Cockerell, 1911
Megachile praedicta Cockerell	Cockerell, 1908b
ROTT, GERMANY (OLIGOCENE)	
Anthidium mortuum (Meunier)	Meunier, 1920; Statz, 1936
Osmia carbonum Heyden	Heyden, 1862
DOMINICAN REPUBLIC (MIOCENE)	
Megachile glaesaria Engel	Present study
OENINGEN, GERMANY (MIOCENE)	
Lithurgus adamiticus (Heer)	Heer, 1865; Cockerell, 1909a
Osmia antiqua Heer	Heer, 1849
Osmia nigra Zeuner and Manning	Zeuner and Manning, 1976
SHANDONG, CHINA (MIOCENE)	
Anthidium basalticum Zhang	Zhang, 1989a
Megachile shanwangae Zhang	Zhang, 1989b
SIBERIA, RUSSIA (MIOCENE)	
Megachile amaguensis Cockerell	Cockerell, 1925b

[a] Of the species listed here, only *M. glaesaria* can be assigned to genus, or even family for that matter, with any degree of confidence. I have seen the types of many of the species (those in the Museum of Comparative Zoology, Harvard University, in 1995 and 1996 and those European species studied by Prof. Zeuner and Dr. Manning that were still in the Department of Palaeontology, Natural History Museum, London, awaiting return to their respective instititutions in 1996) and in most cases they should probably be relegated to "Apoidea incertae sedis."

[b] The species proposed by Germar (1849) as *Apiaria dubia* was tranferred to *Osmia* by Giebel (1856). There is no reason to believe that this specimen was a megachilid; for instance, Pictet (1854) considered it more similar to *Bombus*!

[c] The presence of apical tubercles on the distalmost metasomal tergum is suggestive of a male; however, *Dianthidium* is characterized by having a short median tubercle between longer laterals, a charachteristic absent in the fossil. The absence of integumental markings is also peculiar. This species should perhaps be referred to *Anthidium* or, more appropriately, to its own genus, but it cannot be a true *Dianthidium*.

major speculations on the diversification of megachilids in the fossil record. It does seem reasonable, however, that the Megachilidae as a whole must be quite ancient. Each of the major bee lineages (i.e., families) probably arose and became differentiated rapidly in the early to mid-Cretaceous, with subsequent diversification within each lineage progressing from that time on (Michener, 1979; Michener and Grimaldi, 1988b; Roig-Alsina and Michener, 1993; Engel, 1996; Grimaldi, 1999). The presence of a meliponine (Michener and Grimaldi, 1998a), a highly derived tribe of apine bees, in Late Cretaceous amber of New Jersey suggests that the cladogenetic events that gave rise to the common ancestors of the Apidae and Megachilidae, respectively, as well as the more basal families, had

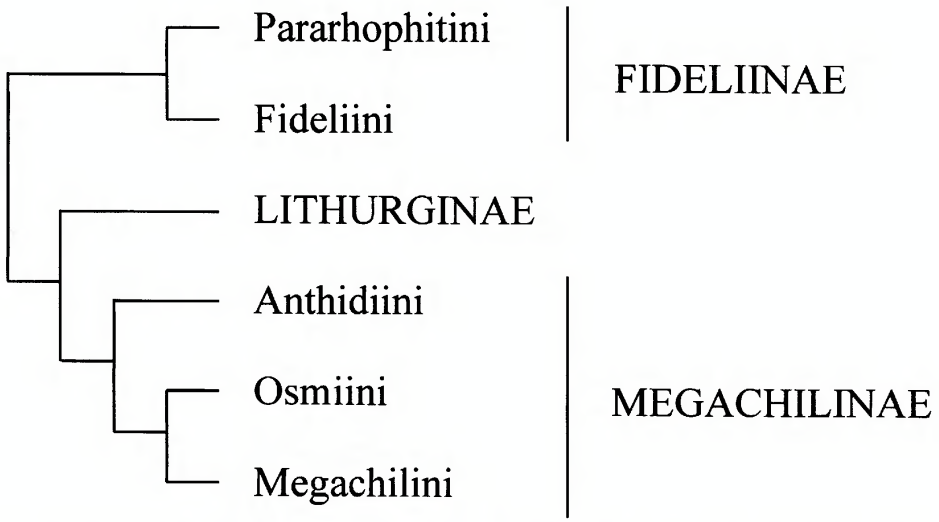

Fig. 4. Phylogeny of family Megachilidae. The tribe Osmiini, as it is currently constituted, is understood to be paraphyletic with respect to Megachilini.

already taken place. This rapid early diversification also accords with the paucity of distinct features uniting subsets of the higher groups, since there would have been little time for a clear hierarchy of characters to develop between the common ancestor of all bees and those of the respective families. It therefore seems apparent that the megachilids as a whole extend well back into the Cretaceous even though the oldest fossils of this family are currently those from the Eocene-Oligocene boundary of Florissant, Colorado. Although this boundary is presently the age at which the oldest megachilid body fossils have been discovered, several authors have reported on fossilized leaves with the distinctive semicircular cuts indicative of megachiline activity (Cockerell, 1908b, 1910; Berry, 1916, 1931; Brooks, 1955; Lewis, 1994). Most of these have been from Eocene sites throughout North America and are slightly older than any of the actual megachilid fossils known. A similarly cut leaf, although not a compression fossil, has been recently recognized from Dominican amber as an inclusion with a specimen of *Sphaerodactylus* (Grimaldi, 1996).

Eickwort et al. (1981) hypothesized that the primitive nesting condition of the Megachilidae was in the soil with subsequent transition to nesting in a plant substrate. This hypothesis is still the best supported position despite Radchenko and Pesenko's (1994) recent arguments to the contrary. Eickwort et al. (1981), using a rudimentary outgroup comparison to form a cladistic interpretation of character evolution in the family, concluded that primitive megachilids nested in the soil and did not apply a lining to the walls of the cells. Radchenko and Pesenko (1994) rejected this hypothesis and considered that the use of a plant substrate is plesiomorphic for the family. This decision was based primarily on (1) the placement of the scopa on the metasomal sterna in megachilids (rather than the hind femora and tibiae of most bees) which these authors consider an adaptation connected with working in a plant substrate; (2) the adaptation of the female mandible for cutting plants; and (3) the hypothesis that nest construction in a plant substrate rather than in the ground is more conducive to the transition of applying plant material to cell walls. Their position seems unjustified. The Fideliinae[4] is presumed to be the basalmost subfamily of the Megachilidae (fig. 4), and this group nests entirely in the soil while sharing the characteristic feature of carrying pollen on the metasoma (Rozen, 1970, 1973, 1977; McGinley and Rozen, 1987), contradicting Radchenko and Pesenko's first prop-

[4] Including tribe Pararhophitini vide Roig-Alsina and Michener (1993).

osition. Furthermore, numerous groups of Megachilinae also nest in the ground (e.g., *Dianthidium*, most *Megachile*, *Osmia*, *Trachusa*, &c.: MacSwain, 1946; Grigarick and Stange, 1968; Eickwort et al., 1981). The modified female mandible for gnawing plant material is not a plesiomorphic feature of the family and seems to have little to do with the early evolution of the Megachilidae. Lastly, there is no reason to believe that the transition to applying plant materials to cell walls was "easier" in a nest already in a plant substrate than one in soil. How the "easiest" path is objectively discovered and whether it is an evolutionary rule is entirely speculative. Soil-nesting is plesiomorphic for the Apoidea ground plan, as well as for each family of bees.

Although *M. glaesaria* is here reported as the first amber megachilid, there have been some amber fossils previously treated as megachilid bees. Menge (1856) and Brischke (1886) reported individuals of *Osmia* and *Chalicodoma*,[5] respectively from Baltic amber. None were named species, and most of their material has not survived to the present day. Similarly, Bachofen-Echt (1949) mentioned specimens of *Megachile* (under the *lapsus*, *Megachila*) and *Osmia* from Baltic amber, but none were described species. I have not yet been able to locate the material upon which these determinations were based and therefore cannot confirm whether or not these were true megachilids. Among named taxa, the peculiar Baltic amber genus *Glyptapis* Cockerell (1909a, b) has been assigned at times as an enigmatic megachilid, although the genus has been shifted several times between this and other families over the past nine decades (e.g., Apidae, Melittidae). From material before me that is referable to *Glyptapis* the genus appears to belong to the Apidae, representing its own lineage within this family (Engel, personal obs.). Presently involved in a monographic study of the Baltic amber bees, I hope that this uncertainty over the position of *Glyptapis* will be clarified in the coming year. With these prior megachilid candidates removed, *M. glaesaria* stands alone as the first true megachilid bee fossil to be discovered as an amber inclusion. Hopefully, it will not be the last.

[5] Owing to the inability of these authors to correctly identify bees, it has to be wondered if these were megachilines at all. For example, surviving material of Menge's work in the British Museum is grossly misplaced even following the taxonomic conventions of his time (Engel, personal obs.).

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